Openness to experience is associated with neural and performance measures of memory in older adults

Running title: Openness in memory-related neural aging

Christopher Stolz[1*], Ariane Bulla[1], Joram Soch[2,3], Björn H. Schott[1,2,4], Anni Richter[1*]

[1] Leibniz Institute for Neurobiology (LIN), Magdeburg, Germany

[2] German Center for Neurodegenerative Diseases (DZNE), Göttingen, Germany

[3] Bernstein Center for Computational Neuroscience (BCCN), Berlin, Germany

[4] Department of Psychiatry and Psychotherapy, University Medical Center Göttingen, Göttingen, Germany

*Correspondence

Anni Richter, Leibniz Institute for Neurobiology, Department of Behavioral Neurology, Brenneckestraße 6, D-39118 Magdeburg, Germany. Email: anni.richter@lin-magdeburg.de. Telephone: 0049-391-626393151.

Christopher Stolz, Leibniz Institute for Neurobiology, Department of Behavioral Neurology, Brenneckestraße 6, D-39118 Magdeburg, Germany. Email: christopher.stolz@lin-magdeburg.de

Statements

Acknowledgments

The authors would like to thank Hartmut Schütze for programming the fMRI paradigm. We thank Anne Assmann, Adriana Barman, Hannah Feldhoff, Larissa Fischer, Marieke Klein, Lea Knopf, Matthias Raschick, Annika Schult for help with behavioral data collection. We are grateful to Kerstin Möhring, Ilona Wiedenhöft, Katja Neumann, and Claus Tempelmann for assistance with MRI data acquisition.

Data Availability Statement

Due to data protection regulations, sharing of the entire data set underlying this study in a public repository is not possible. We have previously provided GLM contrast images as a NeuroVault collection (https://neurovault.org/collections/QBHNSRVW/) and MATLAB code for imaging scores as a GitHub repository (https://github.com/JoramSoch/FADE_SAME) for an earlier article using the same dataset (Soch, Richter, Schütze, Kizilirmak, Assmann, Behnisch, et al., 2021). Access to de-identified raw data will be provided by the authors upon reasonable request.

Funding and Conflict of Interest declaration

The work was supported by the European Regional Development Fund and the State of Saxony-Anhalt (Research Alliance "Autonomy in Old Age") and by the Deutsche Forschungsgemeinschaft (CRC 1436/ A05 to C.S. and B.H.S.). The funding agencies had no role in the design or analysis of the study. The authors have no conflict of interest, financial or otherwise, to declare.

Abstract

Age-related decline in episodic memory performance is a well-replicated finding across numerous studies. Recent studies focusing on aging and individual differences found that the Big Five personality trait Openness to Experience is associated with better episodic memory performance in older adults, but the associated neural mechanisms are largely unclear. Here we investigated the relationship between Openness and memory network function in a sample of 352 participants (104 older adults, 50-80 years; 209 young adults, 18-35 years). Participants underwent functional magnetic resonance imaging (fMRI) during a visual memory encoding task. Functional memory brain-network integrity was assessed using the SAME scores (similarity of activations during memory encoding), which reflect the deviation of a participant's memory network activity from prototypical fMRI activity patterns of young adults. Openness was assessed using the NEO Five Factor Inventory (NEO-FFI). Older vs. young adults showed lower memory performance and higher deviation of fMRI activity patterns (i.e., lower SAME scores). Specifically in older adults, high Openness was associated with better memory performance, and mediation analysis showed that this relationship was partially mediated by higher SAME scores. Our results suggest that trait Openness may constitute a protective factor in cognitive aging by better preservation of the brain's memory network.

Keywords: openness to experience, episodic memory, aging, fMRI, subsequent memory effect

Abstract word count: 200

The total number of words in the text (excluding references, tables and figure legends): 4886

Introduction

Episodic memory is often defined as the ability to encode and recall information of experienced previous events (Baddeley, 2001; Tulving, 2002). A decline in episodic memory performance has been widely characterized as a hallmark symptom of a number of age-related neurological conditions, particularly Alzheimer's disease (AD; Tromp *et al.*, 2015; El Haj *et al.*, 2016), but it has also been associated with neurocognitive aging in healthy adults (Cansino, 2009; Salthouse, 2010; Grady, 2012). Despite the age-related episodic memory decline, there is considerable interindividual variability in memory performance in older adults, presumably due to protective factors for age-related neurocognitive declines (Cansino, 2009), such as physical activity (Lee *et al.*, 2010; Bherer *et al.*, 2013), education (Hendrie *et al.*, 2006), and intelligence capacities (Bråthen *et al.*, 2021). At personality trait level, the Big Five trait Openness to Experience (hereafter: Openness) has been associated with episodic memory performance (Gregory *et al.*, 2010; Terry *et al.*, 2013; Curtis *et al.*, 2015; Luchetti *et al.*, 2016; Sutin *et al.*, 2019), with older adults scoring high in this trait showing better memory performance. While the association between Openness and episodic memory performance in older adults is a well-replicated finding, the underlying brain processes are still largely unknown.

In neuroimaging studies, episodic memory encoding and retrieval have been associated with activations of the medial temporal lobe system (MTL; i.e., hippocampus, parahippocampal and perirhinal cortex), as well as of prefrontal, parietal, and occipital cortices (Davachi, 2006; Rugg and Vilberg, 2013; Nenert *et al.*, 2014). These regions are also subject to age-related structural changes in both grey and white matter volumes (Raz and Rodrigue, 2006; Head *et al.*, 2008; Fjell and Walhovd, 2010), although results are mixed regarding the relationship between age-related structural differences and cognitive performance (Salthouse, 2011; Oschwald *et al.*, 2019). This may in part be due to individual differences in compensatory mechanisms to

maintain cognitive abilities, which may be less reflected by structural changes (Raz and Lindenberger, 2011; Cabeza *et al.*, 2018; Tang *et al.*, 2018; Bråthen *et al.*, 2021). In contrast, age-related memory deficits are typically accompanied by differences in functional brain-network activity in older compared to young adults (Düzel *et al.*, 2011; Maillet and Rajah, 2014; Fjell *et al.*, 2016; Damoiseaux, 2017; Soch, Richter, Schütze, Kizilirmak, Assmann, Behnisch, *et al.*, 2021; Soch, Richter, Schütze, Kizilirmak, Assmann, Knopf, *et al.*, 2021). In a meta-analysis on age-related differences in brain activity during subsequent memory tasks, Maillet & Rajah (2014) reported that memory-related MTL activity was invariant between young and older adults. However, occipital and fusiform cortices were under-recruited in older adults, whereas prefrontal cortices and midline brain structures like the precuneus showed higher activations – or reduced deactivations with aging.

To quantify the degree of age-related deviation of fMRI activation patterns from prototypical activity in young adults, single-value scores of activation (and deactivation) patterns during episodic memory encoding have been proposed (Düzel *et al.*, 2011; Soch, Richter, Schütze, Kizilirmak, Assmann, Behnisch, *et al.*, 2021). Düzel et al. (2011) described the FADE score (functional activity deviation during encoding), a measure of deviation from prototypical memory network activity. More recently, Soch, Richter, Schütze, Kizilirmak, Assmann, Behnisch, et al. (2021) introduced the SAME score (similarity of activations during memory encoding), which measures similarity with prototypical brain activations of young adults and reflects both brain activation and deactivation patterns. The SAME score correlates positively with memory performance in older adults, that is, higher similarity of encoding-related activations is predictive for better episodic memory performance. This holds for dependent measures (i.e. obtained from the same fMRI task; Soch, Richter, Schütze, Kizilirmak, Assmann, Behnisch, *et al.*, 2021) as well as for independent measures (i.e. using distinct neuropsychological testing; for a preprint see Richter *et al.*, 2022) of memory performance. As

a reductionist measure, the SAME score is suitable for investigating correlations with other variables like personality traits (Allen and DeYoung, 2015; DeYoung and Allen, 2019).

Openness reflects the tendency to be creative, imaginative, curious, and open to new ideas and art (Costa and McCrae, 1989). Highly open individuals have been characterized to show a predisposition towards cognitive flexibility and exploration (DeYoung *et al.*, 2005; DeYoung, 2013; DeYoung, 2015). Openness is considered a highly cognitive trait (DeYoung, 2013; DeYoung, 2014) and has been linked to better performance in cognitive abilities such as working memory, inhibitory control, as well as fluid and crystallized intelligence (DeYoung *et al.*, 2005; Chamorro-Premuzic and Furnham, 2008). An fMRI study showed that trait Openness was related to working memory accuracy and this effect was fully mediated by activity in left lateral prefrontal and medial frontal cortices (DeYoung *et al.*, 2009). In addition to replicating the positive relationship between Openness and intelligence measures, Soubelet & Salthouse (2010) reported that individuals scoring high on trait Openness also showed better episodic memory performance. Large cohort studies examined links between individual differences in Big Five personality traits and age-related episodic memory performance. In a meta-analysis focusing on older adults (>50 years), Luchetti et al. (2016) reported that high Openness, high Conscientiousness, and low Neuroticism were associated with better memory performance and lower memory decline over a four-year longitudinal follow-up. The cross-sectional result pattern was replicated in another sample (Sutin *et al.*, 2019), and another longitudinal study showed that individuals scoring high on Openness and low on Neuroticism performed better in an episodic memory task 20 years later (Stephan *et al.*, 2020). While there were slightly different correlation patterns of Big Five personality traits and episodic memory performance among those studies, low Neuroticism and high Openness were consistently reported to be associated with better memory performance in older adults. This overall supports the notion of trait Openness as a potential protective factor (and Neuroticism a potential risk factor) for memory function in aging.

While there is evidence supporting a relationship of better episodic memory performance in older adults with both high trait Openness and better preserved episodic memory brain-network activity, it is yet unclear whether brain activity patterns could serve as a link between individual differences in Openness and memory performance. To this end, the present study aimed to investigate the relationship between Openness, episodic memory performance, and neural episodic memory encoding in young and older adults using personality assessment and fMRI in a visual memory encoding task. Based on previous studies, we hypothesized that trait Openness would be positively related to (1) episodic memory performance and (2) the perserved levels of memory brain-network activity (i.e. higher SAME scores) in older adults. Moreover, we also want to answer the question if (3) the relationship between trait Openness and episodic memory performance is mediated by the levels of memory brain-network activity in older adults. While the present study focuses on Openness and memory contrasts, we additionally explored other Big Five personality traits and fMRI novelty contrasts.

Methods

Participants

We investigated and combined two previously described study cohorts of 117 (Assmann *et al.*, 2021) and 259 (Soch, Richter, Schütze, Kizilirmak, Assmann, Knopf, *et al.*, 2021) healthy adults. As we were interested in personality traits, participants were included only if personality questionnaire data were available. These personality attributes have not been analysed or published previously. The total sample of 352 adults was split up into groups of young (n = 209, 18 to 35 years old; age M = 24.30, SD = 3.29) and older adults (n = 143, 50 to 80 years old; age M = 63.80, SD = 6.68). Participants were recruited via flyers at the local academic institutes, advertisement in local newspapers and during public events of the Leibniz Institute for Neurobiology (e.g. *Long Night of the Sciences*). All participants were right-handed, fluent in German language, and did not report any neurological or mental disorder in a standardized neuropsychiatric interview. The local ethics committee of the Faculty of Medicine at the Otto von Guericke University Magdeburg approved the study. All participants signed informed consent in accordance with the Declaration of Helsinki (World Medical Association, 2013) and received financial compensation for participation.

Visual memory encoding task

In an fMRI session, participants performed an incidental visual memory encoding task (Düzel *et al.*, 2018; Assmann *et al.*, 2021; Soch, Richter, Schütze, Kizilirmak, Assmann, Knopf, *et al.*, 2021). More specifically, participants viewed images of indoor and outdoor scenes and were asked to classify the photos as indoor or outdoor via button press. The task consisted of 132 trials, including unknown indoor and outdoor images (44 trials each; "novel" images) and two

images which were pre-familiarized to the participants (one indoor, one outdoor, each presented in 22 trials; "master" images). Each trial started with the presentation of an image for 2500 ms followed by a fixation cross for a variable delay between 500 to 2300 ms in the first cohort (Assmann *et al.*, 2021) and 700 to 2650 ms in the second cohort (Soch, Richter, Schütze, Kizilirmak, Assmann, Knopf, *et al.*, 2021).

Approximately 70 minutes after the start of the fMRI session, participants underwent a surprise recognition memory test outside the scanner. In this test, the 88 images from the fMRI session ("old") and 44 at this time unknown images ("new") were presented. Participants were asked to rate the familiarity of each image on a Likert scale from 1 ("definitely new") to 5 ("definitely old"). Data were collected using custom code written in Presentation (Version 0.55, Neurobehavioral Systems, www.neurobs.com).

Memory performance score A'

The memory performance score (A') was calculated based on the recognition ratings collected in the recognition memory test. To this end, the hit rate of old stimuli and false alarm rate of the new stimuli were quantified as functions of the rating thresholds. The final memory performance score A' then was computed as the area under the curve (AUC) of the hit rate as a function of the false alarm rate. A' ranged from 0 to 1 with A' = 0.5 indicating random guessing and A' = 1 perfect performance (i.e., perfect hit rate and no false alarms). The exact calculation of A' is described in the appendix of Soch, Richter, Schütze, Kizilirmak, Assmann, Behnisch, et al. (2021).

fMRI data acquisition and preprocessing

The fMRI data were assessed using two Siemens 3T MR tomographs (Verio and Skyra). Functional MRI was assessed as 206 T2*-weighted echo-planar images (EPIs; first cohort: TR = 2.4 s, TE = 30 ms, flip-α = 80°; 40 slices, 104 x 104 in-plane resolution, voxel size = 2 x 2 x 3 mm, for details see Assmann et al., 2021; second cohort: TR = 2.58 s, TE = 30 ms, flip-α = 80°; 47 slices, 64 x 64 in-plane resolution, voxel size = 3.5 x 3.5 x 3.5 mm, for details see Soch, Richter, Schütze, Kizilirmak, Assmann, Knopf, et al., 2021) in interleaved-ascending slice order (1, 3, … 47, 2, 4, …, 46). Structural MRI was acquired as a T1-weighted MPRAGE image (TR = 2.5 s, TE = 4.37 ms, flip-α= 7°; 192 slices, 256 ×256 in-plane resolution, voxel size = 1 x 1 x 1 mm) for later co-registration.

Data preprocessing and analysis were performed using Statistical Parametric Mapping (SPM12; Wellcome Trust Center for Neuroimaging, University College London, London, UK; https://www.fil.ion.ucl.ac.uk/spm/software/spm12/). EPIs were corrected for acquisition delay, head motion, and in the second cohort additionally for magnetic field inhomogeneities using voxel-displacement maps derived from the field maps. Finally, unwarped EPIs were normalized to a common voxel size of 3 x 3 x 3 mm and eventually spatially smoothed using an isotropic Gaussian kernel of 6 mm at FWHM.

Extraction of single-value FADE and SAME fMRI scores

FADE and SAME scores were calculated following the protocol of previous studies (Soch, Richter, Schütze, Kizilirmak, Assmann, Behnisch, *et al.*, 2021; Soch, Richter, Schütze, Kizilirmak, Assmann, Knopf, *et al.*, 2021; also see the preprint of Richter *et al.*, 2022). First, a reference voxel pattern of interest was defined based on significant fMRI novelty (contrasting novel with familiar images) and memory (parametrically modulating the BOLD response to

novel images as a function of later remembering or forgetting) contrasts within young adults. Second, for every participant and fMRI contrast, the FADE score (indicating the deviation of activations from young subjects) and the SAME score (indicating the similarity of activations and deactivations with young subjects) score was calculated to characterize the agreement of each participants' activity pattern with prototypical fMRI activity patterns seen in young subjects. For a detailed description of the FADE and SAME score calculation, see Soch, Richter, Schütze, Kizilirmak, Assmann, Behnisch, et al. (2021). Hereafter, we refer to the scores as follows:

- FADE score computed from the novelty contrast: FADE novelty score;

- SAME score computed from the novelty contrast: SAME novelty score;

- FADE score computed from the memory contrast: FADE memory score;

- SAME score computed from the memory contrast: SAME memory score.

Assessment of trait Openness to Experience

Openness which reflects self-reports of being imaginative, curious, and having a wide range of interests was assessed using the German version (Borkenau and Ostendorf, 1993; Körner *et al.*, 2008) of the NEO-Five Factor Inventory (NEO-FFI; Costa and McCrae, 1989). The NEO-FFI is a 60-item questionnaire (12 items for each scale) that measures the Big Five personality traits Neuroticism, Extraversion, Openness, Agreeableness, and Conscientiousness. The items are rated on a five-point Likert scale (strongly disagree to strongly agree). The internal consistency of the scales ranged between a Cronbach's alpha of 0.71 and 0.85 (Borkenau and Ostendorf, 1993; Schmitz *et al.*, 2001; Körner *et al.*, 2008).

Since previous studies reported substantial covariations of Openness with demographic variables and a range of cognitive functions (DeYoung *et al.*, 2005; Gregory *et al.*, 2010; Soubelet and Salthouse, 2010), we included age, gender (male vs. female), education (with vs.

without German university entrance diploma, "Abitur"), and crystallized intelligence measured with the Multiple-Choice Vocabulary Intelligence Test (Mehrfachwahl-Wortschatz-Intelligenztest B [MWT-B]; Lehrl, 1999) as covariates in the analyses.

Statistical analysis

Data were analyzed using custom code written in MATLAB R2022a and IBM® SPSS® Statistics, Version 28. Comparisons of mean A', FADE/SAME novelty and memory scores and personality scores between young vs. older adults were performed using t tests. For nominally-scale variables (gender and education), the χ^2-test for independence was used. All reported correlation coefficients were Pearson's r if not stated otherwise. To examine the independent effects of Openness on A' and the FADE/SAME memory scores in older adults, multiple regression analyses were calculated including Openness, age, gender, education, and MWT-B scores as explanatory variables. Mediation models with Openness as independent variable, A' as dependent variable, and FADE/SAME memory scores as mediator variable were calculated using the *lavaan* package (Rosseel, 2012) in R (R Core Team, 2013). The reported path estimates for the mediation model were standardized estimates using all path information (Std.all). The reported effect sizes were standardized beta coefficients (β) and Cohen's d.

As an exploratory analysis, we computed voxel-wise regressions of the fMRI subsequent memory contrast with Openness in older adults. Results are reported at $p_{\text{cluster}} < 0.05$ using family-wise error rate (FWE) cluster-level correction and an uncorrected cluster-forming threshold of $p_{\text{voxel}} < 0.001$ (Eklund *et al.*, 2016).

Results

Demographic information and trait Openness

As reported previously, older adults vs. young adults less frequently had an university entrance diploma ("Abitur"; for discussion see Soch, Richter, Schütze, Kizilirmak, Assmann, Behnisch, et al., 2021). In the NEO-FFI, older adults showed lower scores for Openness, Neuroticism, and Extraversion, and higher scores for Conscientiousness compared to young adults (Table 1).

Table 1

Demographic information and mean (SD) personality trait scores in the young vs. older adult groups

Variable	Young adults	Older adults	Test statistics
Age	24.30 (3.29)	63.80 (6.68)	$t = 65.49, p < 0.001$
Gender	112/97	87/56	$\chi^2 = 1.82, p = 0.178$
	f/m	f/m	
Education (Abitur)	203/6	65/78	$\chi^2 = 124.79, p < 0.001$
	with/without	with/without	
Neuroticism	28.53 (6.39)	27.09 (5.34)	$t = 2.28, p = 0.023$
Extraversion	42.33 (5.35)	40.01 (4.82)	$t = 4.16, p < 0.001$
Openness	43.14 (5.74)	40.97 (4.51)	$t = 3.97, p < 0.001$
Agreeableness	46.17 (5.40)	45.61 (4.38)	$t = 1.08, p = 0.283$
Conscientiousness	45.66 (6.09)	47.50 (5.25)	$t = 2.94, p = 0.004$

Age differences for memory performance and FADE/SAME scores

A' was significantly lower in older (M = 0.77, SD = 0.73) vs. young adults (M = 0.81, SD = 0.75; $t(350) = 5.20$, $p < 0.001$, $d = 0.57$). As shown in Figure 1, there was a significant difference between older vs. young adults in the FADE (young: M = -1.30, SD = 0.57; older: M = -0.86, SD = 0.50; $t(350) = 7.38$, $p < 0.001$, $d = 0.80$) and SAME memory scores (young: -0.07, SD = 0.85; older: M = -1.13, SD = 0.53; $t(350) = 13.17$, $p < 0.001$, $d = 1.43$). Taken together, this suggests a higher deviation (FADE) and lower similarity (SAME) of the memory brain-network activity in older adults compared to the reference of prototypical young adult activity with a particularly large effect size for the SAME score. While the SAME novelty score was significantly different between the age groups (young: -0.08, SD = 0.71; older: M = -0.39, SD = 0.54; $t(350) = 4.43$, $p < 0.001$, $d = 0.48$), there was no significant group difference in the FADE novelty score (young: M = -1.77, SD = 0.66; older: M = -1.89, SD = 0.62; $t(350) = 1.73$, $p = 0.084$, $d = 0.19$; for a discussion, see Soch, Richter, Schütze, Kizilirmak, Assmann, Behnisch, et al., 2021).

Figure 1. Violin plots of the FADE/SAME (A) memory and (B) novelty scores in young vs. older adults. The white dot indicates the mean value and the box outlines the interquartile range and median. *** $p < 0.001$

Correlations of performance and imaging scores with big five personality traits

While we observed significant correlations between the FADE/SAME memory scores with A' in both age groups, personality scores particularly correlated with memory performance and

fMRI scores in older adults (Table 2). Largest correlations were found for Openness with A' ($r = 0.27$, $p = 0.001$), FADE ($r = -0.25$, $p = 0.002$) and SAME memory scores ($r = 0.29$, $p < 0.001$), suggesting that older adults scoring high on Openness show better memory performance and more prototypical memory network activity (Figure 2). In the exploratory analysis for the other personality traits, a similar pattern was observed for Extraversion (Table 2).

Table 2

Correlation coefficients between the Big Five personality traits and the memory performance (A') and fMRI scores for the young and older adults

		Neur.	Extr.	Open.	Agre.	Cons.	A'
Young adults	A'	-0.07	0.17**	0.09	0.14*	0.04	1
	FADE memory score	-0.04	-0.07	-0.03	-0.14	-0.04	-0.27**
	SAME memory score	-0.03	0.05	0.04	0.10	-0.01	0.39**
	FADE novelty score	-0.09	0.11	0.07	0.06	0.03	0.09
	SAME novelty score	0.04	-0.06	-0.09	-0.12	-0.08	0.02
Older adults	A'	-0.14	0.25**	0.27**	0.01	-0.02	1
	FADE memory score	0.01	-0.17*	-0.25**	0.11	0.10	-0.33**
	SAME memory score	0.01	0.17*	0.29**	-0.07	-0.13	0.41**
	FADE novelty score	-0.04	0.04	0.12	0.15	-0.07	-0.04
	SAME novelty score	-0.01	0.13	-0.09	-0.03	0.15	0.24**

Notes. Neur. = Neuroticism, Extr. = Extraversion, Open. = Openness to Experience, Agre. = Agreeableness, Cons. = Conscientiousness. ** $p < 0.01$, * $p < 0.05$

Figure 2. Scatter plots including 95% confidence intervals and the data distribution for the correlations of Openness (here shown as z scores) with (A) the memory performance and (B) the SAME memory score within the group of older adults.

Trait Openness within the group of older adults

As Openness was correlated with A' and the FADE/SAME memory scores in older adults only, further analyses are focused on this group. In older adults, Openness was significantly positively correlated with education (point-biserial $r = 0.22$, $p = 0.008$) and MWT-B test results ($r = 0.18$, $p = 0.036$), but not with age ($r = 0.04$, $p = 0.658$) or gender (point-biserial $r = -0.04$, $p = 0.656$). Multiple regression analyses revealed that there was a substantial direct effect of Openness on A', FADE memory score and SAME memory score, independently of the demographic variables and MWT-B scores (Table 3).

Table 3

Multiple regression analysis of the direct effects of Openness on memory performance and FADE/SAME memory scores controlled for demographic variables and crystallized intelligence in older adults

	A'		FADE memory score		SAME memory score	
	β	*p*	β	*p*	B	*p*
Openness	0.24**	0.005	-0.22*	0.009	0.26**	0.002
Age	-0.10	0.250	0.17*	0.048	-0.09	0.297
Gender	0.03	0.730	-0.07	0.415	0.15	0.075
Education	0.09	0.321	-0.11	0.213	0.18*	0.048
MWT-B	0.10	0.288	-0.09	0.351	0.03	0.707

Notes. One participant was excluded from all analyses involving the MWT-B due to missing value. ** $p < 0.01$, * $p < 0.05$

As shown in Table 4, the mediation analysis with the FADE memory score as mediator on the relationship between Openness as independent variable and A' as dependent variable revealed a partial mediation effect (total effect: $\beta = 0.27$, $p = 0.001$; indirect effect: $\beta = 0.07$, $p = 0.020$). This suggests that the FADE memory score mediated 26.29% of the total effect between Openness and A'. See supplementary material A for mediation analyses including Extraversion, which did not reach statistical significance.

The mediation analysis with the SAME memory score as mediator on the relationship between Openness as independent variable and A' as dependent variable also revealed a partial mediation effect (total effect: $\beta = 0.27$, $p = 0.001$; indirect effect: $\beta = 0.11$, $p = 0.004$; Table 4, Figure 3). This suggests that the SAME memory score mediated 40.74% of the total effect between Openness and A'.

To ensure the observed mediation effects were not due to covariations with demographics and crystallized intelligence, the analyses described above were also conducted for Openness, A', FADE/SAME memory scores adjusted for age, gender, and MWT-B scores. We were able to confirm the partial mediation effects in these additional analyses (supplementary material B).

Table 4

Mediation analysis within the group of older adults with FADE/SAME memory scores as mediators of the association between Openness and episodic memory performance (A').

FADE memory score	β	P
Total effect: Openness → A'	0.27	0.001
Direct effect: FADE memory score → A'	-0.25	0.002
Direct effect: Openness → A'	0.20	0.013
Indirect effect: Openness → FADE memory score → A'	0.07 (26.29%)	0.020
SAME memory score	β	P
Total effect: Openness → A'	0.27	0.001
Direct effect: SAME memory score → A'	0.37	< 0.001
Direct effect: Openness → A'	0.16	0.036
Indirect effect: Openness → SAME memory score → A'	0.11 (40.74%)	0.004

Mediation model in older adults (N = 143)

Total effect: 0.27**
Indirect effect: 0.11** (partial mediation 40.74%)

Figure 3. Mediation analysis within the group of older adults shows that the relationship between trait Openness and the memory performance (A') is partly mediated (40.74% of the total effect) by the SAME memory fMRI score. *$p < 0.05$; **$p < 0.01$.

Voxel-wise association of fMRI contrasts with Openness

As an exploratory analysis, we computed voxel-wise regressions of the fMRI memory contrast with Openness in older adults. We observed significantly positive associations of Openness with successful memory encoding activations in left (β = 0.21, SD = 0.20; $t(141) = 4.35$, $p = 0.009$, x y z = -42 -79 23; 47 voxels) and right (β = 0.08, SD = 0.16; $t(141) = 4.15$, $p = 0.025$, x y z = 33 -79 2; 38 voxels) medial occipital gyrus (MOG; FWE cluster-level correction; Figure 4A). Additionally, the analysis revealed a hint for an association with the precuneus/posterior cingulate cortex (β = 0.14, SD = 0.25), which however did not reach corrected statistical significance ($t(141) = 4.50$, $p = 0.080$, x y z = 15 -58 17, 28 voxels; FWE cluster-level correction; supplementary material C, Figure S1).

Correlations between the left and right MOG peak voxel activity and personality traits as well as the FADE/SAME memory scores and A' are shown in Table 5 and Figure 4B. A mediation analysis including Openness as independent, A' as dependent, and left MOG peak voxel activity

as mediation variable revealed a partial mediation (total effect: β = 0.27, *p* = 0.001; indirect effect: β = 0.09, *p* = 0.01, 33.33% of the total effect). Openness was positively related to A' (β = 0.18, *p* = 0.03), and left MOG (β = 0.34, *p* < 0.001). There was a significant positive association between left MOG and A' (β = 0.26, *p* = 0.002).

A Openness & fMRI memory effect

B Mediation model with left MOG in older adults (N = 143)

Total effect: 0.27**
Indirect effect: 0.09* (partial mediation 33.33%)

Figure 4. (A) Regression analysis of Openness and fMRI memory effect (positive effect) in older adults. *p* < 0.05, FWE-corrected at cluster level, cluster-defining threshold *p* < 0.001, uncorrected. All activation maps are superimposed on the MNI template brain provided by MRIcroGL (https://www.nitrc.org/projects/mricrogl/). (B) Mediation analysis showed that

the relationship between Openess and memory performance (A') was partially mediated (33.33% of the total effect) by activity in the left MOG. *$p < 0.05$; **$p < 0.01$.

Table 5

Pearson's correlations between occipital gyrus peak-voxel activity (left & right MOG), Big Five personality traits, and memory-related brain activity and performance.

	left MOG		right MOG	
	r	*p*	*r*	*p*
Neuroticism	0.04	0.615	-0.15	0.079
Extraversion	0.16	0.061	0.10	0.242
Openness	0.34***	< 0.001	0.33**	< 0.001
Agreeableness	-0.01	0.905	0.04	0.667
Conscientiousness	-0.05	0.556	0.05	0.527
FADE memory score	-0.47***	< 0.001	-0.37***	< 0.001
SAME memory score	0.42***	< 0.001	0.31***	< 0.001
Memory performance A'	0.33***	< 0.001	0.07	0.440

Notes. *** $p < 0.001$

Discussion

The goal of the present study was to investigate to what extent differences in memory encoding-related brain activity explain the frequently reported relationship between Openness and memory performance in older adults. To this end, trait Openness was correlated with single-value fMRI scores reflecting deviations from or similarities with prototypical memory encoding brain activity in a visual memory encoding task. Consistent with our hypotheses, high trait Openness in older adults was related to both, better memory performance and more prototypical brain activity (low FADE/high SAME score). A mediation analysis revealed that the relationship between Openness and memory performance in older adults was substantially mediated by FADE/SAME fMRI scores. This overall provides first evidence that the relationship between Openness and better memory performance in older adults substantially depends on more prototypical memory brain-network activity.

Mediation of Openness and episodic memory performance by neural activity

Across all subjects, age group (older vs. young adults) had a significant effect on episodic memory performance and memory-related fMRI activity as indicated by FADE and SAME scores. This converges with previous studies demonstrating age differences in memory performance and functional brain activity (Düzel *et al.*, 2011; Maillet and Rajah, 2014; Fjell *et al.*, 2016; Damoiseaux, 2017; Morcom and Henson, 2018; Soch, Richter, Schütze, Kizilirmak, Assmann, Behnisch, *et al.*, 2021; Soch, Richter, Schütze, Kizilirmak, Assmann, Knopf, *et al.*, 2021).

The link between Openness and episodic memory retrieval in older adults was mediated by activity in memory brain networks during memory encoding. Specifically, older adults who

scored high in trait Openness also showed more prototypical brain-network activity during memory encoding, which was directly related to better episodic memory performance. These results converge with studies reporting a positive relationship between Openness and episodic memory performance in older adults (Terry *et al.*, 2013; Luchetti *et al.*, 2016; Sutin *et al.*, 2019; Stephan *et al.*, 2020). One possible explanation for this may be that highly Open older adults are more likely to engage into intellectually stimulating activities such as travelling, attending cultural events, seeking novel or aesthetic experiences (Kraaykamp and van Eijck, 2005; Chamorro-Premuzic and Furnham, 2008; Soubelet and Salthouse, 2010; Jackson *et al.*, 2020; Talpain and Soubelet, 2022). Additionally, Openness is related to a broad range of cognitive abilities that are of high relevance for cognitive reserve, including fluid and crystallized intelligence, and working memory capacity (Gregory *et al.*, 2010; Schretlen *et al.*, 2010; Sharp *et al.*, 2010; Chapman *et al.*, 2012; Nishita *et al.*, 2019). Moreover, aspects of cognitive reserve capacity are overlapping with reports on how high Openness in older adults is indicating preservation of episodic memory functioning (Franchow *et al.*, 2013). Despite anatomical prerequisites of the brain, increased exposure to cognitive-stimulating life experiences may delay age-, and disease-related manifestation of memory deficits (Stern *et al.*, 2019). In this context, high Openness may reflect an index of cognitive functioning at personality trait level and overall contribute to a higher cognitive reserve in neurocognitive aging. While the present study cannot ultimately explain, which mechanism specifically drives the relationship between Openness and memory performance, it nevertheless adds a neurocognitive dimension to it.

Exploratory analysis: Associations between Openness and medial occipital brain activity

In an exploratory voxel-wise analysis within older adults, we found that high Openness and better memory performance were related to amplified activations in the MOG. Converging with our results, the MOG shows robust activations during encoding (Maillet and Rajah, 2014) and

recognition (Yonelinas *et al.*, 2001) as well as increased functional connectivity with the hippocampus during successful memory formation (Ranganath *et al.*, 2005). Hence, the MOG is considered part of a visual memory and perception network, which is active during both episodic memory encoding and retrieval (Slotnick, 2004; Slotnick and Schacter, 2006; Thakral and Slotnick, 2015; Waldhauser *et al.*, 2016). This is in line with a proposed model for visual memory encoding, which demonstrated an early involvement of the MOG driven by the primary and secondary visual areas (Nenert *et al.*, 2014). These areas are also affected by aging, indicating decreased occipital activity during working memory, visual attention, and episodic retrieval tasks (Cabeza *et al.*, 2004; Davis *et al.*, 2008), and a disproportionate recruitment of left vs. right visual cortex during encoding of visual episodic information (Maillet and Rajah, 2014). There is preliminary evidence suggesting that high Openness is related to different low-level visual perceptual experiences (Antinori *et al.*, 2017). Accordingly, Blake & Palmisano (2021) reported differences in perceptual processing of ambiguous visual stimuli in high creativity/divergent thinking, two features which are also related to individual differences in Openness (DeYoung *et al.*, 2012; Kaufman *et al.*, 2016). This overall raises the question whether the age-related associations between Openness and successful memory encoding may not only rely on preserving neurocognitive functioning by intellectual engagement and activities, but also on personality-related differences in early visual processing during memory encoding.

In addition to the positive relationship between Openness and memory-related MOG activity, we found hints for the involvement of activity in the precuneus/posterior cingulate cortex. The precuneus has previously been associated with self-related and social cognition (Gusnard *et al.*, 2001; Soch *et al.*, 2017), episodic memory retrieval (Cavanna and Trimble, 2006; Hebscher *et al.*, 2018), creative cognition (Beaty *et al.*, 2014; Benedek *et al.*, 2014; Shofty *et al.*, 2022), and long-term visual memory formation (Gilmore *et al.*, 2015; Brodt *et al.*, 2018; Schott *et al.*, 2019). Older compared to young adults commonly show reduced deactivations or even atypical

activations of cortical midline structures like the precuneus and posterior cingulate cortex, which was also related to impaired memory performance (Miller *et al.*, 2008; Düzel *et al.*, 2011; Maillet and Rajah, 2014; Billette *et al.*, 2022). Despite the robustness of these findings, the underlying neural mechanisms are still largely unknown. Some authors point out the possibility that increased encoding-related DMN activation may reflect a compensatory mechanism (Desgranges *et al.*, 2011; Andrews-Hanna *et al.*, 2014; Maillet and Rajah, 2014; Mohan *et al.*, 2016; Mak *et al.*, 2017). It is conceivable that the precuneus might play a role in preserving memory-related brain function in highly open older adults. However, this should be considered a cautious interpretation of the present results and warrants further research. Future studies in personality neuroscience of aging could assess the role of the precuneus in the aging trajectories of high vs. low open individuals by investigating interactions of personality and functional brain activity on memory changes in a longitudinal manner. Supplementary material C offers additional discussions on the relationship of Openness and activity in the default mode network.

Clinical relevance

In a recent meta-analysis, AD patients showed lower levels of self-reported and informant-obtained Openness and Extraversion, and higher levels of Neuroticism compared to controls (D'Iorio *et al.*, 2018). A similar personality profile was considered a risk factor and predictor for developing AD (Caselli et al. 2018; Duberstein *et al.*, 2011) and assumed to change before vs. after the AD diagnosis (Robins Wahlin and Byrne, 2011). Other studies proposed that specifically low Openness was a pre-clinical marker of incipient cognitive decline (Williams *et al.*, 2013), and that high Openness may protect from memory decline (Terry *et al.*, 2013). This suggests that Openness is part of a personality profile in which high Openness may constitute a protective factor in the transition from healthy memory functioning to risk-stages for AD and personality changes that go along the development of AD. Our study is thus of high clinical

relevance, as it provides novel evidence that the presumably protective effect of Openness on episodic memory functioning is reflected by functional brain-network differences. This should encourage conducting similar studies in individuals at risk of developing AD to better understand the beneficial characteristics of personality traits on brain alterations before and after AD onset.

A potential role for the mesolimbic dopamine system and Openness in preserved cognition

In the present study, memory network activity and performance in older adults were both specifically correlated with Openness and Extraversion, which potentially may emphasize the influence of the dopamine system. This converges with empirical and theoretical references that ascribe dopaminergic functioning a major role in the cognitive and behavioral expressions of Openness and Extraversion (Depue and Lenzenweger, 2001; DeYoung, 2010; DeYoung, 2013; Pickering and Pesola, 2014; Wacker and Smillie, 2015). Extraversion has previously been linked to dopamine-rich brain regions (Li *et al.*, 2019) and cortical reward processing (Cooper *et al.*, 2014; Smillie *et al.*, 2019). In a recent pharmacological study, Openness and divergent thinking were linked to dopamine activity (Käckenmester *et al.*, 2019). Furthermore, in the cybernetic big five theory, Openness and Extraversion are considered a meta-trait Plasticity whose neuromodulator is dopamine (DeYoung *et al.*, 2005; DeYoung, 2013; DeYoung, 2015). Dopamine has also often been implicated in episodic memory functioning (Wittmann *et al.*, 2005; Adcock *et al.*, 2006; Düzel *et al.*, 2010), and impaired dopaminergic neurotransmission is associated with cognitive aging and longitudinal memory decline (Bäckman and Farde, 2009; Morcom *et al.*, 2010; Chowdhury *et al.*, 2012; Papenberg *et al.*, 2014; Nyberg *et al.*, 2016). Düzel et al. (2010) proposed that an increase of mesolimbic dopaminergic activity promotes exploratory behavior and ultimately memory performance in older adults. In line with this

framework, our results suggest links between Openness/Extraversion and age-related differences in neural memory functioning.

Relevance of Openness facets

A major limitation of the present study was that personality traits were assessed with only one questionnaire (NEO-FFI), which ultimately did not allow to examine by which trait sub-facet the age-related Openness effects on memory were mainly driven. Accordingly, previous studies reported that Openness facets (e.g. fantasy, feelings, ideas) had different longitudinal trajectories (Bleidorn *et al.*, 2009) and varying associations with psychometric intelligence (Moutafi *et al.*, 2006). Other studies that divided Openness into the sub-facets "Openness" (fantasy, aesthetics) and "Intellect" (intellectual engagement; DeYoung, 2014) linked Intellect to creative achievements in the sciences (Kaufman *et al.*, 2016), fluid intelligence (Nusbaum and Silvia, 2011), and increased working memory-related prefrontal activity (DeYoung *et al.*, 2009). In contrast, the sub-facet Openness, but not Intellect was related to implicit learning (Kaufman *et al.*, 2010) and reduced cortical thickness in fronto-temporal gyri (Vartanian *et al.*, 2018). According to the independent associations of Openness sub-facets with individual differences at cognitive, behavioral, and neural levels, it seems very encouraging for follow-up studies to assess personality traits with a higher resolution (e.g. NEO-PI-R or Big Five Aspects Scale, BFAS; DeYoung, 2007). Such studies would not only provide a better understanding of the Openness sub-facets, but would also shed more light on the specific cognitive processes (e.g. creativity vs. intellect) involved in the protective effects of Openness on neurocognitive aging. In the context of the present study, it might be conceivable that the effects of Openness on cortical memory encoding and memory performance may be even stronger represented in one of the facets than the global Openness domain.

Specificity of trait activation

The associations of Openness with neural memory encoding were only supported in the older adult age group. This might be due to group-related differences in average Openness and memory performance. In line with other research, in the present study, older vs. young adults showed lower Openness scores (Schaie *et al.*, 2004; Roberts *et al.*, 2006; Allemand *et al.*, 2007; Bleidorn *et al.*, 2009) and a declined memory performance (Oschwald *et al.*, 2019). It is conceivable that the memory task was not challenging enough for young adults, such that it did not pose an optimal situation to activate the influences of personality traits (McNaughton and Smillie, 2018; Taconnat *et al.*, 2022) and thus masked potential shared variance between memory encoding and trait Openness. Moreover, the FADE/SAME scores are by definition contrasted with the memory-related fMRI activity of the young group. Thereby, the FADE/SAME scores might further conceal potential trait correlations within the group of young adults and rather reflect highly suitable single-scores for the investigation of personality in neurocognitive aging.

Conclusion

Our study provides novel evidence that the personality trait Openness is associated with episodic memory performance and this effect was substantially mediated by memory-related brain-network activity in older adults. Specifically, those older adults with high Openness showed better memory performance and this was due to a higher similarity to brain activity patterns of young adults. To the best knowledge of the authors, this is the first report linking the relationship between trait Openness and memory performance to actual brain activity in an episodic memory task. The present study further shows the utility of single-value fMRI scores in personality neuroscience with a high statistical power.

References

Adcock, R.A., Thangavel, A., Whitfield-Gabrieli, S., et al. (2006). Reward-Motivated Learning: Mesolimbic Activation Precedes Memory Formation. *Neuron*, **50**, 507–17

Allemand, M., Zimprich, D., Hertzog, C. (2007). Cross-sectional age differences and longitudinal age changes of personality in middle adulthood and old age. *Journal of Personality*, **75**, 323–58

Allen, T.A., DeYoung, C.G. (2015). Personality Neuroscience and the Five Factor Model. *Oxford Handbook of the Five Factor Model*, 1–62

Andrews-Hanna, J.R., Smallwood, J., Spreng, R.N. (2014). The default network and self-generated thought: component processes, dynamic control, and clinical relevance. *Annals of the New York Academy of Sciences*, **1316**, 29–52

Antinori, A., Carter, O.L., Smillie, L.D. (2017). Seeing it both ways: Openness to experience and binocular rivalry suppression. *Journal of Research in Personality*, **68**, 15–22

Assmann, A., Richter, A., Schütze, H., et al. (2021). Neurocan genome-wide psychiatric risk variant affects explicit memory performance and hippocampal function in healthy humans. *European Journal of Neuroscience*, **53**, 3942–59

Association, W.M. (2013). World Medical Association Declaration of Helsinki: ethical principles for medical research involving human subjects. *Jama*, **310**, 2191–94

Bäckman, L., Farde, L. (2009). *Role of Dopamine Systems in Cognitive Aging*.

Baddeley, A. (2001). The concept of episodic memory. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **356**, 1345–50

Beaty, R.E., Benedek, M., Wilkins, R.W., et al. (2014). Creativity and the default network: A functional connectivity analysis of the creative brain at rest. *Neuropsychologia*, **64**, 92–

Benedek, M., Jauk, E., Fink, A., et al. (2014). To create or to recall? Neural mechanisms underlying the generation of creative new ideas. *NeuroImage*, **88**, 125–33

Bherer, L., Erickson, K.I., Liu-Ambrose, T. (2013). A review of the effects of physical activity and exercise on cognitive and brain functions in older adults. *Journal of Aging Research*, **2013**

Billette, O. V., Ziegler, G., Aruci, M., et al. (2022). Novelty-Related fMRI Responses of Precuneus and Medial Temporal Regions in Individuals at Risk for Alzheimer Disease. *Neurology*, **99**, E775–88

Blake, A., Palmisano, S. (2021). Divergent Thinking Influences the Perception of Ambiguous Visual Illusions. *Perception*, **50**, 418–37

Bleidorn, W., Kandler, C., Riemann, R., et al. (2009). Patterns and Sources of Adult Personality Development: Growth Curve Analyses of the NEO PI-R Scales in a Longitudinal Twin Study. *Journal of Personality and Social Psychology*, **97**, 142–55

Borkenau, P., Ostendorf, F. (1993). *NEO-Fünf-Faktoren Inventar (NEO-FFI) [NEO-Five Factor Inventory]*. Göttingen: Hogrefe Verlag.

Bråthen, A.C.S., De Lange, A.M.G., Fjell, A.M., et al. (2021). Risk- and protective factors for memory plasticity in aging. *Aging, Neuropsychology, and Cognition*, **28**, 201–17

Brodt, S., Gais, S., Beck, J., et al. (2018). Fast track to the neocortex: A memory engram in the posterior parietal cortex. *Science*, **362**, 1045–48

Cabeza, R., Albert, M., Belleville, S., et al. (2018). Maintenance, reserve and compensation: the cognitive neuroscience of healthy ageing. *Nature Reviews Neuroscience*, **19**, 701–10

Cabeza, R., Daselaar, S.M., Dolcos, F., et al. (2004). Task-independent and Task-specific Age

Effects on Brain Activity during Working Memory, Visual Attention and Episodic Retrieval. *Cerebral Cortex*, **14**, 364–75

Cansino, S. (2009). Episodic memory decay along the adult lifespan: A review of behavioral and neurophysiological evidence. *International Journal of Psychophysiology*, **71**, 64–69

Cavanna, A.E., Trimble, M.R. (2006). The precuneus: A review of its functional anatomy and behavioural correlates. *Brain*, **129**, 564–83

Chamorro-Premuzic, T., Furnham, A. (2008). Personality, intelligence and approaches to learning as predictors of academic performance. *Personality and Individual Differences*, **44**, 1596–1603

Chapman, B., Duberstein, P., Tindle, H.A., et al. (2012). Personality predicts cognitive function over 7 years in older persons. *American Journal of Geriatric Psychiatry*, **20**, 612–21

Chowdhury, R., Guitart-Masip, M., Bunzeck, N., et al. (2012). Dopamine modulates episodic memory persistence in old age. *Journal of Neuroscience*, **32**, 14193–204

Cooper, A.J., Duke, Ã., Pickering, A.D., et al. (2014). Individual differences in reward prediction error: contrasting relations between feedback-related negativity and trait measures of reward sensitivity, impulsivity and extraversion. *Frontiers in Human Neuroscience*, **8**

Costa, P.T., McCrae, R.R. (1989). *NEO five-factor inventory (NEO-FFI)*. Odessa, FL: Psychological Assessment Resources.

Curtis, R.G., Windsor, T.D., Soubelet, A. (2015). The relationship between Big-5 personality traits and cognitive ability in older adults - A review. *Aging, Neuropsychology, and Cognition*, **22**, 42–71

D'Iorio, A., Garramone, F., Piscopo, F., et al. (2018). Meta-Analysis of Personality Traits in Alzheimer's Disease: A Comparison with Healthy Subjects. *Journal of Alzheimer's Disease*, **62**, 773–87

Damoiseaux, J.S. (2017). Effects of aging on functional and structural brain connectivity. *NeuroImage*, **160**, 32–40

Davachi, L. (2006). Item, context and relational episodic encoding in humans. *Current Opinion in Neurobiology*, **16**, 693–700

Davis, S.W., Dennis, N.A., Daselaar, S.M., et al. (2008). Qué PASA? the posterior-anterior shift in aging. *Cerebral Cortex*, **18**, 1201–9

Depue, R.A., Lenzenweger, M.F. (2001). A neurobehavioral dimensional model. In: *Handbook of personality disorders: Theory, research, and treatment.* p. 136–76.

Desgranges, B., Mevel, K., Chételat, G., et al. (2011). The default mode network in healthy aging and Alzheimer's disease. *International Journal of Alzheimer's Disease*, **2011**

DeYoung, C.G. (2007). *Big Five Aspects Scale: BFAS*.

DeYoung, C.G. (2015). Cybernetic Big Five Theory. *Journal of Research in Personality*, **56**, 33–58

DeYoung, C.G. (2014). Openness/Intellect: a dimension of personality reflecting cognitive exploration. *APA handbook of personality and social psychology: Personality processes and individual differences*, **4**, 369–99

DeYoung, C.G. (2013). The neuromodulator of exploration: A unifying theory of the role of dopamine in personality. *Frontiers in Human Neuroscience*, **7**, 1–26

DeYoung, C.G. (2010). Toward a theory of the big five. *Psychological Inquiry*, **21**, 26–33

DeYoung, C.G., Allen, T.A. (2019). Personality neuroscience: A developmental perspective.

Handbook of Personality Development, 79–105

DeYoung, C.G., Grazioplene, R.G., Peterson, J.B. (2012). From madness to genius: The Openness/Intellect trait domain as a paradoxical simplex. *Journal of Research in Personality*, **46**, 63–78

DeYoung, C.G., Peterson, J.B., Higgins, D.M. (2005). Sources of Openness/Intellect: Cognitive and neuropsychological correlates of the fifth factor of personality. *Journal of Personality*, **73**, 825–58

DeYoung, C.G., Shamosh, N.A., Green, A.E., et al. (2009). Intellect as Distinct From Openness: Differences Revealed by fMRI of Working Memory. *Journal of Personality and Social Psychology*, **97**, 883–92

Duberstein, P.R., Chapman, B.P., Tindle, H.A., et al. (2011). Personality and Risk for Alzheimer's Disease in Adults 72 Years of Age and Older: A 6-Year Follow-Up. *Psychology and Aging*, **26**, 351–62

Düzel, E., Berron, D., Schütze, H., et al. (2018). CSF total tau levels are associated with hippocampal novelty irrespective of hippocampal volume. *Alzheimer's and Dementia: Diagnosis, Assessment and Disease Monitoring*, **10**, 782–90

Düzel, E., Bunzeck, N., Guitart-Masip, M., et al. (2010). NOvelty-related Motivation of Anticipation and exploration by Dopamine (NOMAD): Implications for healthy aging. *Neuroscience and Biobehavioral Reviews*, **34**, 660–69

Düzel, E., Schütze, H., Yonelinas, A.P., et al. (2011). Functional phenotyping of successful aging in long-term memory: Preserved performance in the absence of neural compensation. *Hippocampus*, **814**, n/a-n/a

Eklund, A., Nichols, T.E., Knutsson, H. (2016). Cluster failure: Why fMRI inferences for spatial extent have inflated false-positive rates. *Proceedings of the National Academy of*

Sciences of the United States of America, **113**, 7900–7905

Fjell, A.M., Sneve, M.H., Storsve, A.B., et al. (2016). Brain Events Underlying Episodic Memory Changes in Aging: A Longitudinal Investigation of Structural and Functional Connectivity. *Cerebral Cortex*, **26**, 1272–86

Fjell, A.M., Walhovd, K.B. (2010). Structural brain changes in aging: Courses, causes and cognitive consequences. *Reviews in the Neurosciences*, **21**, 187–221

Franchow, E.I., Sauchy, Y., Thorgusen, S.R., et al. (2013). More than Education: Openness to Experience Contributes to Cognitive Reserve in Older Adulthood. *Journal of Aging Science*, **01**, 1–8

Gilmore, A.W., Nelson, S.M., McDermott, K.B. (2015). A parietal memory network revealed by multiple MRI methods. *Trends in Cognitive Sciences*, **19**, 534–43

Grady, C. (2012). The cognitive neuroscience of ageing. *Nature Reviews Neuroscience*, **13**, 491–505

Gregory, T., Nettelbeck, T., Wilson, C. (2010). Openness to experience, intelligence, and successful ageing. *Personality and Individual Differences*, **48**, 895–99

Gusnard, D.A., Akbudak, E., Shulman, G.L., et al. (2001). Medial prefrontal cortex and self-referential mental activity: Relation to a default mode of brain function. *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 4259–64

El Haj, M., Antoine, P., Amouyel, P., et al. (2016). Apolipoprotein E (APOE) ε4 and episodic memory decline in Alzheimer's disease: A review. *Ageing Research Reviews*, **27**, 15–22

Head, D., Rodrigue, K.M., Kennedy, K.M., et al. (2008). Neuroanatomical and Cognitive Mediators of Age-Related Differences in Episodic Memory. *Neuropsychology*, **22**, 491–507

Hebscher, M., Levine, B., Gilboa, A. (2018). The precuneus and hippocampus contribute to individual differences in the unfolding of spatial representations during episodic autobiographical memory. *Neuropsychologia*, **110**, 123–33

Hendrie, H.C., Albert, M.S., Butters, M.A., et al. (2006). The NIH Cognitive and Emotional Health Project. *Alzheimer's and Dementia*, **2**, 12–32

Jackson, J.J., Hill, P.L., Payne, B.R., et al. (2020). Linking openness to cognitive ability in older adulthood: The role of activity diversity. *Aging and Mental Health*, **24**, 1079–87

Käckenmester, W., Bott, A., Wacker, J. (2019). Openness to experience predicts dopamine effects on divergent thinking. *Personality Neuroscience*, **2**

Kaufman, S.B., DeYoung, C.G., Gray, J.R., et al. (2010). Implicit learning as an ability. *Cognition*, **116**, 321–40

Kaufman, S.B., Quilty, L.C., Grazioplene, R.G., et al. (2016). Openness to Experience and Intellect Differentially Predict Creative Achievement in the Arts and Sciences. *Journal of Personality*, **84**, 248–58

Körner, A., Drapeau, M., Albani, C., et al. (2008). Deutsche Normierung des NEO-Fünf-Faktoren-Inventars (NEO-FFI)German Norms for the NEO-Five Factor Inventory. *Zeitschrift fuer Medizinische Psychologie*, **17**, 133–44

Kraaykamp, G., van Eijck, K. (2005). Personality, media preferences, and cultural participation. *Personality and Individual Differences*, **38**, 1675–88

Lee, Y., Back, J.H., Kim, J., et al. (2010). Systematic review of health behavioral risks and cognitive health in older adults. *International Psychogeriatrics*, **22**, 174–87

Lehrl, S. (1999). *Mehrfachwahl-Wortschatz-Intelligenztest: MWT-B*. Balingen: Spitta.

Li, M., Wei, D., Yang, W., et al. (2019). Neuroanatomical correlates of extraversion: A test-

retest study implicating gray matter volume in the caudate nucleus. *NeuroReport*, **30**, 953–59

Luchetti, M., Terracciano, A., Stephan, Y., et al. (2016). Personality and cognitive decline in older adults: Data from a longitudinal sample and meta-analysis. *Journals of Gerontology - Series B Psychological Sciences and Social Sciences*, **71**, 591–601

Maillet, D., Rajah, M.N. (2014). Age-related differences in brain activity in the subsequent memory paradigm: A meta-analysis. *Neuroscience and Biobehavioral Reviews*, **45**, 246–57

Mak, L.E., Minuzzi, L., MacQueen, G., et al. (2017). The Default Mode Network in Healthy Individuals: A Systematic Review and Meta-Analysis. *Brain Connectivity*, **7**, 25–33

McNaughton, N., Smillie, L.D. (2018). Some Metatheoretical Principles for Personality Neuroscience. *Personality Neuroscience*, **1**, e11

Miller, S.L., Celone, K., DePeau, K., et al. (2008). Age-related memory impairment associated with loss of parietal deactivation but preserved hippocampal activation. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 2181–86

Mohan, Akansha, Roberto, A.J., Mohan, Abhishek, et al. (2016). The significance of the Default Mode Network (DMN) in neurological and neuropsychiatric disorders: A review. *Yale Journal of Biology and Medicine*, **89**, 49–57

Morcom, A.M., Bullmore, E.T., Huppert, F.A., et al. (2010). Memory encoding and dopamine in the aging brain: A psychopharmacological neuroimaging study. *Cerebral Cortex*, **20**, 743–57

Morcom, A.M., Henson, R.N.A. (2018). Increased prefrontal activity with aging reflects nonspecific neural responses rather than compensation. *Journal of Neuroscience*, **38**,

7303–13

Moutafi, J., Furnham, A., Crump, J. (2006). What facets of openness and conscientiousness predict fluid intelligence score? *Learning and Individual Differences*, **16**, 31–42

Nenert, R., Allendorfer, J.B., Szaflarski, J.P. (2014). A model for visual memory encoding. *PLoS ONE*, **9**

Nishita, Y., Tange, C., Tomida, M., et al. (2019). Positive effects of openness on cognitive aging in middle-aged and older adults: A 13-year longitudinal study. *International Journal of Environmental Research and Public Health*, **16**

Nusbaum, E.C., Silvia, P.J. (2011). Are Openness and Intellect distinct aspects of Openness to Experience? A test of the O/I model. *Personality and Individual Differences*, **51**, 571–74

Nyberg, L., Karalija, N., Salami, A., et al. (2016). Dopamine D2 receptor availability is linked to hippocampal-caudate functional connectivity and episodic memory. *Proceedings of the National Academy of Sciences of the United States of America*, **113**, 7918–23

Oschwald, J., Guye, S., Liem, F., et al. (2019). Brain structure and cognitive ability in healthy aging: A review on longitudinal correlated change. *Reviews in the Neurosciences*, **31**, 1–57

Owsley, C. (2016). Vision and Aging. *Annual review of vision science*, **2**, 255–71

Papenberg, G., Li, S.C., Nagel, I.E., et al. (2014). Dopamine and glutamate receptor genes interactively influence episodic memory in old age. *Neurobiology of Aging*, **35**, 1213.e3-1213.e8

Pickering, A.D., Pesola, F. (2014). Modeling dopaminergic and other processes involved in learning from reward prediction error: contributions from an individual differences perspective. *Frontiers in Human Neuroscience*, **8**, 1–20

Ranganath, C., Heller, A., Cohen, M.X., et al. (2005). Functional connectivity with the hippocampus during successful memory formation. *Hippocampus*, **15**, 997–1005

Raz, N., Lindenberger, U. (2011). Only time will tell: Cross-sectional studies offer no solution to the age-brain-cognition triangle: Comment on salthouse (2011). *Psychological Bulletin*, **137**, 790–95

Raz, N., Rodrigue, K.M. (2006). Differential aging of the brain: Patterns, cognitive correlates and modifiers. *Neuroscience and Biobehavioral Reviews*, **30**, 730–48

Richter, A., Soch, J., Kizilirmak, J.M., et al. (2022). Summary statistics of memory-related fMRI activity reflect dissociable neuropsychological and anatomical signatures of neurocognitive aging. *bioRxiv Neuroscience*

Roberts, B.W., Walton, K.E., Viechtbauer, W. (2006). Patterns of mean-level change in personality traits across the life course: A meta-analysis of longitudinal studies. *Psychological Bulletin*, **132**, 1–25

Robins Wahlin, T.B., Byrne, G.J. (2011). Personality changes in Alzheimer's disease: A systematic review. *International Journal of Geriatric Psychiatry*, **26**, 1019–29

Rosseel, Y. (2012). lavaan: An R package for Structural Equation Modeling. *Journal of Statistical Software*, **48**, 1–36

Rugg, M.D., Vilberg, K.L. (2013). Brain networks underlying episodic memory retrieval. *Current Opinion in Neurobiology*, **23**, 255–60

Salthouse, T.A. (2011). Neuroanatomical substrates of age-related cognitive decline. *Psychological Bulletin*, **137**, 753–84

Salthouse, T.A. (2010). Selective review of cognitive aging. *Journal of the International Neuropsychological Society*, **16**, 754–60

Schaie, K.W., Willis, S.L., Caskie, G.I.L. (2004). The Seattle Longitudinal Study: Relationship between personality and cognition. *Aging, Neuropsychology, and Cognition*, **11**, 304–24

Schmitz, N., Hartkamp, N., Baldini, C., et al. (2001). Psychometric properties of the German version of the NEO-FFI in psychosomatic outpatients. *Personality and Individual Differences*, **31**, 713–22

Schott, B.H., Wüstenberg, T., Lücke, E., et al. (2019). Gradual acquisition of visuospatial associative memory representations via the dorsal precuneus. *Human Brain Mapping*, **40**, 1554–70

Schretlen, D.J., Van Der Hulst, E.J., Pearlson, G.D., et al. (2010). A neuropsychological study of personality: Trait openness in relation to intelligence, fluency, and executive functioning. *Journal of Clinical and Experimental Neuropsychology*, **32**, 1068–73

Sharp, E.S., Reynolds, C.A., Pedersen, N.L., et al. (2010). Cognitive Engagement and Cognitive Aging: Is Openness Protective? *Psychology and Aging*, **25**, 60–73

Shofty, B., Gonen, T., Bergmann, E., et al. (2022). The default network is causally linked to creative thinking. *Molecular Psychiatry*, **27**, 1848–54

Slotnick, S.D. (2004). Visual memory and visual perception recruit common neural substrates. *Behavioral and cognitive neuroscience reviews*, **3**, 207–21

Slotnick, S.D., Schacter, D.L. (2006). The nature of memory related activity in early visual areas. *Neuropsychologia*, **44**, 2874–86

Smillie, L.D., Jach, H.K., Hughes, D.M., et al. (2019). Extraversion and reward-processing: Consolidating evidence from an electroencephalographic index of reward-prediction-error. *Biological Psychology*, **146**

Soch, J., Deserno, L., Assmann, A., et al. (2017). Inhibition of information flow to the default mode network during self-reference versus reference to others. *Cerebral Cortex*, **27**, 3930–42

Soch, J., Richter, A., Schütze, H., Kizilirmak, J.M., Assmann, A., Behnisch, G., et al. (2021). A comprehensive score reflecting memory-related fMRI activations and deactivations as potential biomarker for neurocognitive aging. *Human Brain Mapping*, **42**, 4478–96

Soch, J., Richter, A., Schütze, H., Kizilirmak, J.M., Assmann, A., Knopf, L., et al. (2021). Bayesian model selection favors parametric over categorical fMRI subsequent memory models in young and older adults. *NeuroImage*, **230**, 117820

Soubelet, A., Salthouse, T.A. (2010). The role of activity engagement in the relations between Openness/Intellect and cognition. *Personality and Individual Differences*, **49**, 896–901

Stephan, Y., Sutin, A.R., Luchetti, M., et al. (2020). Personality and memory performance over twenty yearas: findings from three prospective studies. *Journal of psychosomatic research*, 1–17

Stern, Y., Barnes, C.A., Grady, C., et al. (2019). Brain reserve, cognitive reserve, compensation, and maintenance: operationalization, validity, and mechanisms of cognitive resilience. *Neurobiology of Aging*, **83**, 124–29

Sutin, A.R., Stephan, Y., Luchetti, M., et al. (2019). Five-factor model personality traits and cognitive function in five domains in older adulthood. *BMC Geriatrics*, **19**, 1–10

Taconnat, L., Pinard, F., Vanneste, S., et al. (2022). Personality traits affect older adults' memory differently depending on the environmental support provided at encoding. *Personality and Individual Differences*, **191**

Talpain, E., Soubelet, A. (2022). Strategy Use Mediates the Relation between Openness to Experience and Episodic Memory in Younger and Older Adults. *Psychological Reports*,

125, 358–74

Tang, L., Shafer, A.T., Ofen, N. (2018). Prefrontal cortex contributions to the development of memory formation. *Cerebral Cortex*, **28**, 3295–3308

Team, R.C. (2013). *R: A language and environment for statistical computing*.

Terry, D.P., Puente, A.N., Brown, C.L., et al. (2013). Openness to experience is related to better memory ability in older adults with questionable dementia. *Journal of Clinical and Experimental Neuropsychology*, **35**, 509–17

Thakral, P.P., Slotnick, S.D. (2015). The sensory timecourses associated with conscious visual item memory and source memory. *Behavioural Brain Research*, **290**, 143–51

Tromp, D., Dufour, A., Lithfous, S., et al. (2015). Episodic memory in normal aging and Alzheimer disease: Insights from imaging and behavioral studies. *Ageing Research Reviews*, **24**, 232–62

Tulving, E. (2002). Episodic Memory : From Mind to Brain. *Annual Review of Psychology*, **53**, 1–25

Vartanian, O., Wertz, C.J., Flores, R.A., et al. (2018). Structural correlates of Openness and Intellect: Implications for the contribution of personality to creativity. *Human Brain Mapping*, **39**, 2987–96

Del Viva, M.M., Agostini, R. (2007). Visual spatial integration in the elderly. *Investigative Ophthalmology and Visual Science*, **48**, 2940–46

Wacker, J., Smillie, L.D. (2015). Trait Extraversion and Dopamine Function. *Social and Personality Psychology Compass*, **9**, 225–38

Waldhauser, G.T., Braun, V., Hanslmayr, S. (2016). Episodic memory retrieval functionally relies on very rapid reactivation of sensory information. *Journal of Neuroscience*, **36**,

251–60

Williams, P.G., Suchy, Y., Kraybill, M.L. (2013). Preliminary evidence for low openness to experience as a pre-clinical marker of incipient cognitive decline in older adults. *Journal of Research in Personality*, **47**, 945–51

Wittmann, B.C., Schott, B.H., Guderian, S., et al. (2005). Reward-related fMRI activation of dopaminergic midbrain is associated with enhanced hippocampus-dependent long-term memory formation. *Neuron*, **45**, 459–67

Yonelinas, A.P., Hopfinger, J.B., Buonocore, M.H., et al. (2001). Hippocampal, parahippocampal and occipital-temporal contributions to associative and item recognition memory: An fMRI study. *NeuroReport*, **12**, 359–63

A

Memory contrast scores

*** (young adults vs. older adults, FADE memory score)

*** (young adults vs. older adults, SAME memory score)

B

Novelty contrast scores

*** (young adults vs. older adults, SAME novelty score)

Mediation model in older adults (N = 143)

SAME memory score

Openness to Experience

memory performance A'

0.29**

0.37**

0.16* (0.27**)

Total effect: 0.27**
Indirect effect: 0.11** (partial mediation 40.74%)

Openness & fMRI memory effect

z = (2 17 23)

4.5

t

B Mediation model with left MOG in older adults (N = 143)

```
                        ┌─────────────────────────┐
                        │        left MOG          │
                        └─────────────────────────┘
              0.34**    ↗                         ↘   0.26**

┌─────────────────────────┐                    ┌─────────────────────────┐
│  Openness to Experience │ ─── 0.18* (0.27**) →│   memory performance    │
│                         │                     │           A'            │
└─────────────────────────┘                    └─────────────────────────┘
```

Total effect: 0.27**
Indirect effect: 0.09* (partial mediation 33.33%)